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ORIGINAL ARTICLE

# Nest Site Preference and Fidelity of Chinese Alligator (*Alligator sinensis*)

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**Abstract** Oviparous female reptiles select nesting sites with optimal ecological factors that contribute to egg development. Chinese alligator (*Alligator sinensis*), an oviparous reptile, is a critically endangered crocodilian with temperature-dependent sex determination. Research on its nesting behavior may facilitate the protection of this species. In this study, we monitored nesting behavior over eight years. We compared selected frequency of nest sites, distance from nest site to water, height from nest site top to the water surface, distance from nest site to human activity region, and canopy density between nest sites on the island and bank. The results showed that 45 nest sites were used by female alligators over eight years and each site was selected from one to 10 times. The selected frequency of nest site occurrence on the island was higher than that on the bank ($P < 0.001$). We observed that 88% of the individual alligators (15/17) showed different degrees of nest site fidelity. However, Chinese alligators might not always be loyal to only one nest site because of environmental changes or interspecific competition at nest sites. Our findings suggest that female alligators prefer to nest at island, which might be because of the nests on the island had a higher canopy density ($P = 0.010$) and were further from the human activity region ($P < 0.001$) than those on the bank did. It would be beneficial to reduce human activities during the breeding season and protect the vegetation of Chinese alligator habitats in the future.

**Keywords** Chinese alligator, ecological factor, nest site preference, nest site fidelity

## 1. Introduction

The microhabitat of nest sites is important for the offspring of oviparous animals (Mitchell *et al.*, 2013) to ensure hatching success (Serafini *et al.*, 2009), and maintain body size (Brown and Shine, 2004), growth rate (Lloyd and Martin, 2004), and sex ratio (Doody *et al.*, 2006). Based on this theory, female usually select optimal nest sites before laying eggs (Resetarits, 1996). A few studies suggest that females prefer nesting in areas with particular physical conditions to improve their fitness (Brown and Shine, 2004; Reedy *et al.*, 2013). Some turtles prefer to lay their eggs in the shade or open areas of the beach (Ali *et al.*, 2005; Kamel and Mrosovsky, 2005; Turkozan *et al.*, 2012). Other species such as snakes and lizards select nest sites with more moist substrates, which significantly increases their body size at hatching (Brown and Shine, 2004; Reedy *et al.*, 2013).

Nest site preference may be maintained for one or more breeding seasons (Janzen and Morjan, 2001; Kamel *et al.*, 2006). When female chose the same site or area during different years, it is called nest site fidelity (Switzer, 1993). This nest choice behavior may influence offspring survival (Lindeman, 1992) and nest site fidelity has been documented in numerous species such as birds (Lindberg and Sedinger, 1997), turtles (Mitrus, 2006; Walde *et al.*, 2007), tuatara (Refsnider *et al.*, 2010), and crocodilians (Elsey *et al.*, 2008).

Chinese alligator (*Alligator sinensis*) is a critically endangered freshwater crocodilian endemic to China (Thorbjarnarson and Wang, 1999). Recent investigations show that there are no more than 130 Chinese alligators

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in the wild and approximately 10,000 captive individuals in Anhui and Zhejiang Province (Thorbjarnarson *et al.*, 2002; Wang Z. *et al.*, 2011). Chinese alligator is an oviparous reptile with temperature-dependent sex determination and, therefore, the breeding success and sex ratio of Chinese alligators might be affected by nest site choice (Chen, 2003; Xia and Jiang, 2005; Zhao *et al.*, 2013; Zhou, 2007). It is believed that studying nesting behavior could facilitate the design of effective strategies to protect endangered animals (Liles *et al.*, 2015; Martin *et al.*, 2012). A recent study indicated that the nest site choice of the Chinese alligator species was affected by the vegetation canopy, sunlight duration, and concealment (Wang J. *et al.*, 2011). However, these results were limited by the short study time (one year) or casual observations and might lead to misunderstandings of the factors affecting nest choice of Chinese alligators. To date, little is known about nest site choice of Chinese alligators over a period of years. Therefore, in this study, we monitored the nesting behavior of Chinese alligators over eight years to determine their nest site selection behavior with the aim of providing valuable information that could aid in designing conservation plans.

## 2. Methods

**2.1 Study area and animals** This study was conducted from 2009 to 2016 in the core breeding area of Changxing Yinjiabian Chinese Alligator Nature Reserve (CYCANR; 30°93′ N, 119°73′ E), which is situated in the county of Changxing, Zhejiang Province, China. This reserve is surrounded by farmland, and the core breeding area was mainly composed of several semi-natural ponds, which are typical habitats of the Chinese alligator (Thorbjarnarson *et al.*, 2002). The total size of the core breeding area was 15 100 $m^2$ including 5800 $m^2$ of land where females built nests. There were approximately 90 captive adult female Chinse alligators in the core breeding area during the study period. Female alligators build nests on the bank of the pond or island during the breeding season.

**2.2 Data analysis** The female alligators built nests during consecutive years or with intervals of several years and produced one clutch in mid-June to late-July in the years they nested. Chinese alligators often build nests and lay eggs between 4:00 a.m. and 8:00 a.m. Therefore, we searched the nests once daily from 9:00 a.m. to 11:00 a.m. and observers maintained a distance of at least 15 meters from the alligators to avoid disturbing them. To evaluate the nest site preference of the Chinese alligator, we measured the following four ecological factors at each nest site: distance from nest to water (m), height from nest site top to the water surface (m), distance from nest to human activity region such as path or farmland (m), and canopy density. The canopy density of each nest site was estimated using a method based on the ArcView GIS (Sun *et al.*, 2005). We compared the selected frequency of nest sites between the bank and island to determine the preference of females using Pearson's Chi-squared test. Then, we performed an independent samples *t*-test to compare the ecological factors of nest sites between the bank and island since all the data followed normal distributions based on the Kolmogorov-Smirnov test. All the statistical analyses were conducted using the statistical package for the social sciences (SPSS) version 20.0 (SPSS Inc., Chicago, IL, USA) and the figures were constructed using Origin 8.0 (OriginLab, Northampton, MA, USA).

Chinese alligators that show nest site fidelity select the same nest site in different years and, therefore, we chose those that laid eggs more than twice from 2011 to 2016 to evaluate the nest site fidelity. We marked 68 female alligators by injecting them with Biomark HPT12 PIT Tags (Biomark, Boise, USA) under the dorsal skin of their tails in September 2010. To mark as many alligators as possible, we blocked the habitat holes of the alligators using wire netting and drained the water in the ponds to catch the alligators using ropes. The female alligators were subsequently released into the pond where they were caught after being marked. The number of the PIT tag of the alligators could be read using the detector (Biomark, Boise, USA), which was fixed at the end of a 5 m long pole. When a nest was found, the observers held the pole to place the detector close to the tail of the alligator guarding her nest. The detector could function when it was less than 0.5 m from the tag.

## 3. Results

During 2009 to 2016, we observed that 45 nest sites were used by female alligators and each nest site was selected one to 10 times (Figure 1). We also observed that some alligators selected a nest that had already been used, dug out the previously laid eggs prior to laying their eggs, and subsequently rebuilt the nest. Furthermore, we found that alligators with different PIT tags guarded the same nest at the same or different times. These behaviors suggested that more than one alligator could select the same site in one year. We recorded 22 events during the study period showing that two to four alligators selected the same nest

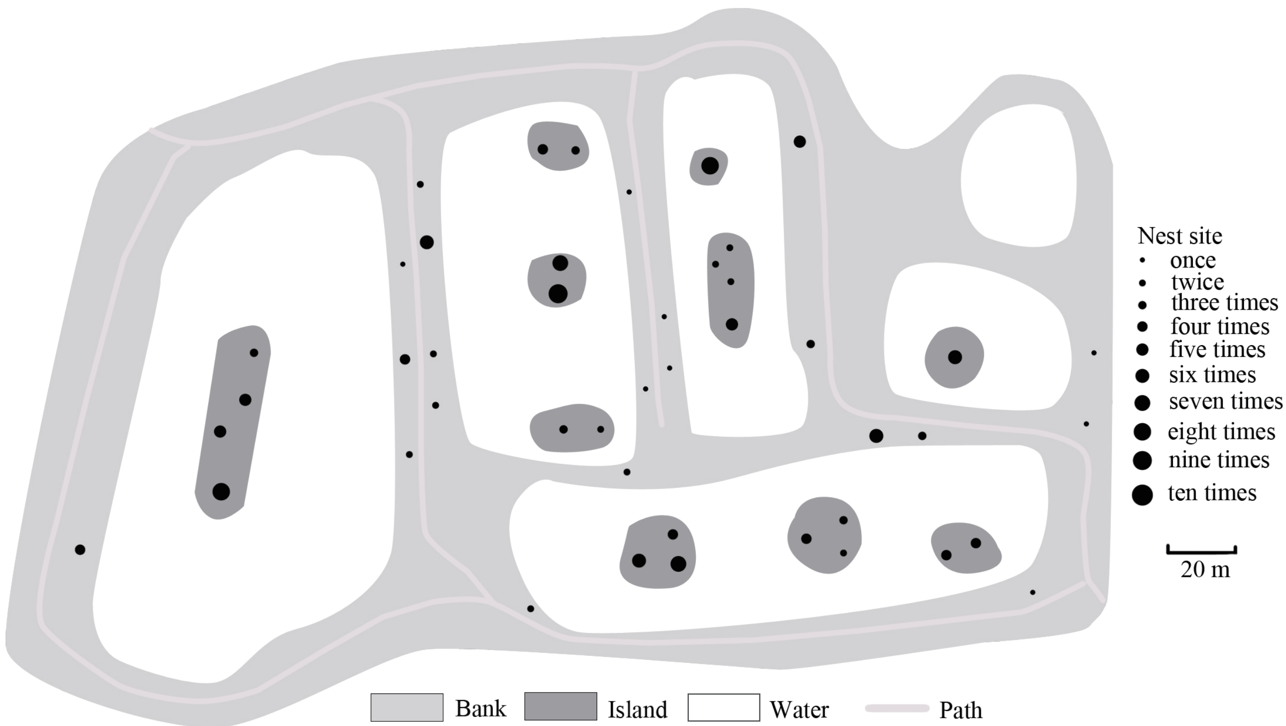


**Figure 1** The distribution of nest sites from 2009 to 2016 in the core breeding area.

site in one year (Table S1). Furthermore, we found that more than half of the nest sites had been used by more than one alligator during the study period. In addition, we observed that 36 of the 68 marked alligators nested one to five times from 2011 to 2016 (Table S1).

There was no nest site located in the area with a canopy density < 0.5 and the canopy openness was 0.84 ± 0.09 ($n$ = 45). These results indicated that Chinese alligators tended to nest in shaded areas. Overall, the mean distance and height from nest sites to the water were 3.1 ± 1.4 m ($n$ = 45). and 0.72 ± 0.30 m ($n$ = 45), respectively. The mean distance from the nests to active human regions was 4.9 ± 4.4 m ($n$ = 45).

Among the 45 nest sites, 21 and 24 were located on the bank and island, respectively (Figure 1). We found that nest sites on the island were used by alligators more frequently than those on the bank were ($\chi^2$ = 44.79, $df$ = 9, $P$ < 0.001, Figure 2). Furthermore, we found that nest sites on the island were significantly further from the region of human activity ($P$ < 0.001) and had a higher canopy density ($P$ = 0.010) than those on the bank did (Table 1). However, there was no significant difference in the other two parameters, distance from nest site to water and height from nest site to the water surface, between nest sites on the bank and the island (Table 1, all $P$ > 0.05).

Among the 36 marked alligators, 17 had nested more than once (Table 2). Fifteen of the 17 alligators exhibited different degrees of fidelity to their nest site while the other two showed no nest site fidelity. Among the 15

**Table 1** Comparison of four ecological factors of nest sites located at bank and island.

| Ecological factors | Mean ± SD | | Statistics | |
|---|---|---|---|---|
| | Island ($n$ = 24) | Bank ($n$ = 21) | $t$ | $P$ |
| Distance from nest site to water (m) | 3.1 ± 1.3 | 3.1 ± 1.5 | 0.019 | 0.985 |
| Height from nest site top to the water surface (m) | 0.73 ± 0.31 | 0.71 ± 0.27 | –0.254 | 0.8 |
| Distance from nest site to human activity area (m) | 7.3 ± 3.9 | 2.0 ± 3.1 | –5.001 | < 0.001 |
| Canopy openness | 0.87 ±0.05 | 0.81 ± 1.1 | –2.689 | 0.01 |

**Table 2** Nest site selection of 17 Chinese alligators from 2011 to 2016.

| Female | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 |
|---|---|---|---|---|---|---|
| YCF-1[a] | S32 | – | S32 | – | – | S32 |
| YCF-38[a] | – | – | – | S17 | – | S17 |
| YCF-115[a] | – | – | S11 | – | S11 | S11 |
| YCF-137[a] | – | S40 | – | – | S40 | – |
| YCF-138[a] | S30 | S30 | S30 | – | S30 | – |
| YCF-140[a] | – | – | – | – | S39 | S39 |
| YCF-141[a] | S5 | S5 | – | – | – | S5 |
| YCF-13[b] | S28 | S28 | – | – | S39 | – |
| YCF-10[b] | S26 | S26 | – | S26 | S27 | S26 |
| YCF-14[b] | S41 | – | S1 | – | S41 | – |
| YCF-53[b] | – | S36 | – | S21 | – | S36 |
| YCF-91[b] | – | S14 | – | S34 | S14 | – |
| YCF-97[b] | – | S29 | S9 | S29 | – | – |
| YCF-103[b] | S29 | S6 | – | – | S6 | – |
| YCF-101[b] | – | S20 | S34 | S20 | S34 | – |
| YCF-11[c] | – | S26 | S18 | – | – | – |
| YCF-61[c] | S37 | S21 | – | – | – | – |

Note: [a] indicates alligator who selected same nest during 2011 to 2016. [b] indicates alligator who selected 2 nest sites during 2011 to 2016. [c] indicates alligator who selected different nest sites during their nesting years. "–" shows that alligator did not nest in the following year.

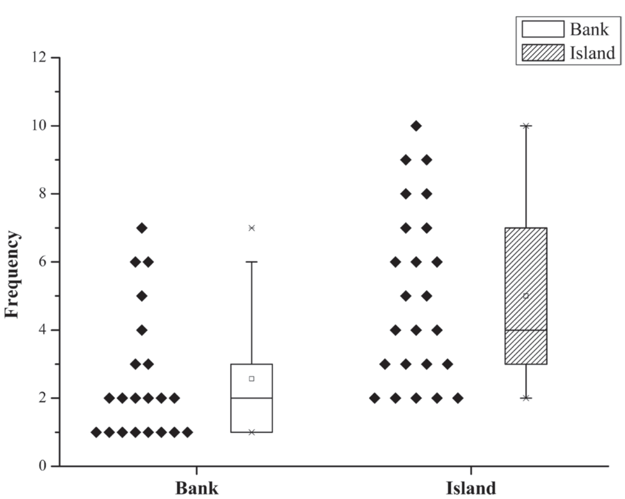


**Figure 2** The selected frequency of nest sites located at bank and island.

alligators, seven that nested two to four times selected the same single nest site during their nesting years. Furthermore, the other eight alligators showed a low loyalty to one nest site since they chose two nest sites while one nest site each was used two to four and one to two times.

## 4. Discussion

Animals often tend to select nest sites with appropriate ecological characteristics that improve the fitness of their offspring (Resetarits, 1996). Although all the nest sites we found had been used by alligators, the frequency of nest site selection by the alligators was obviously different, ranging from one to 10. In this study, we observed that different individuals frequently selected the same nest site in the same or a different year, which implies that Chinese alligators might prefer nest sites with specific ecological factors.

Our results showed that female alligators preferred to nest on the island compared to the bank based on the selected frequency of nest sites (Figure 2). This might be due to the different ecological factors of nest sites in the two areas, and there was evidence of a significant difference in canopy density and distance from nest

sites to human activity regions (Table 1). Therefore, we speculated that the female alligators preferred to select nest sites that were far away from the human activity regions with a high canopy density. The distance from nest sites to human activity regions reflected the security of the nest site (Zhang *et al.*, 2006). Nests that are closer to human activity regions could be destroyed intentionally or unintentionally by humans during the entire hatching time (Thorbjarnarson and Wang, 1999). The Chinese alligators were sensitive to the human disturbance and, therefore, they preferentially selected nest sites far away from regions with human activity.

The canopy density was another factor that attracted alligators to the selected nest sites on the island. For animals with temperature-dependent sex determination, both high and low temperatures in nests could seriously bias the sex ratio of hatchings (Lang and Andrews, 1994). We believed that animals could adjust nest temperature by selecting nest sites with different ecological factors to balance the sex ratio. Kamel (2013) found that canopy density was considered a key factor in the nest site choice of animals with temperature-dependent sex determination because of its effect on the thermal state of the nest. Some animals had been proven to nest in exposed places when the air temperature is low and shaded places when the air temperature is high to ensure the nest temperature was warm enough and avoid overheating, which could compensate for the climate effects on sex ratio (Doody *et al.*, 2006; Ewert *et al.*, 2005). The canopy density has also been proven to be an important factor affecting the nest site choice of Chinese alligators (Zhang *et al.*, 2006). Another study indicated that adult female alligators chose nests according to different thermal properties to adjust the population sex ratio (Zhao *et al.*, 2013). In the last 50 years, the air temperature in China has increased by 0.6–1.1°C (Zhao *et al.*, 2003). This phenomenon could explain why the Chinese alligators chose more nest sites on the island because it has a higher vegetation canopy than that of the bank. It could aid Chinese alligators in adapting to the climate changes and compensate for the effects of climate on sex ratios.

Nest site fidelity has been proven to exist widely in numerous species (Switzer, 1993). This is the first time we directly observed nest site fidelity in Chinese alligators by marking individuals. We found that 15 of the 17 (88%) female alligators that nested at least twice showed nest site fidelity to differing degrees, suggesting this might be a common behavior in Chinese alligators. Based on our observation, we speculated that the high nest site fidelity in this population might be the result of both active and forced nest site selection. We recorded that 45 nest sites had been used by alligators from 2009 to 2016 (Table S1). Furthermore, 15 and 11 females nested in 2015 and 2016, respectively (Table S1). Because of the low number of breeding females, there are several nest sites for each breeding female to choose from, suggesting that nest site fidelity may be due to females selecting the same site actively in the investigated years. However, when the number of breeding females was relatively high in years such as in 2009, 2010, and 2012, the frequency at which different females used the same nest site was relatively high (Table S1). This observation implies there were not enough suitable nest sites in these years and some alligators may have been forced to reuse the same sites even when they were not optimum.

Our results demonstrate that Chinese alligators are not always strictly loyal to one nest site based on the evidence that eight of the 15 alligators used two nest sites for laying eggs three to four times. Some models and studies have proposed that animals change nest sites when ecological characteristics change or more optimal sites are discovered (Lindeman, 1992; Martin *et al.*, 2012; Mitrus, 2006; Switzer, 1993). We found that some tagged alligators such as YCF-97 changed nest sites during the year when they experienced disturbances during the nesting period. However, they reused the original nest site the following year when the disturbance was eliminated. Moreover, we observed that there was an intraspecific competition for nest sites, and some females were forced to choose a new nest site when the old one was being used by other alligators (Table S1). Interestingly, our results showed that some alligators might have two favored nest sites. For instance, YCF-101 selected two nest sites twice from 2012 to 2015. Although seven alligators used only one nest site during different breeding seasons, we were not sure if these Chinese alligators could exhibit fidelity to one site over a prolonged period.

## 5. Conclusion

Our results indicate that Chinese alligators preferred to choose nest sites with a relatively high canopy density that were far away from the human activity regions, such as the island. Furthermore, our study suggests that nest site fidelity might be a common behavior in Chinese alligators, which may be influenced by environmental changes and intraspecific competition. Human disturbance and canopy density were the two key factors that affected the nest site choice of Chinese alligators based on our observations. Therefore, it would be necessary to reduce

human activities during the breeding season and protect the vegetation of the habitat. The results of this study might aid in the development of strategies to recover habitats and select reintroduction area for Chinese alligators.

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## Appendix

**Table S1** Nest site selection of female alligators during 2009 to 2016.

| Nest site | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | Frequency |
|---|---|---|---|---|---|---|---|---|---|
| S1 | - | - | - | - | YCF-14 | - | - | - | 1 |
| S2 | - | - | - | 1 N | - | - | - | - | 1 |
| S3 | - | 1 N | 1 N | 1 N | - | - | - | - | 3 |
| S4 | - | - | 1 N | - | 1 N | - | - | - | 2 |
| S5 | 4 N | 1N | YCF-141 | YCF-141 | - | - | - | YCF-141 | 8 |
| S6 | 1 N | - | - | YCF-103 | - | - | YCF-103 | - | 3 |
| S7 | 1 N | 1 N | - | - | - | - | - | - | 2 |
| S8 | - | - | - | 1 N | 1 N | - | - | - | 2 |
| S9 | - | - | - | - | YCF-97 | - | - | - | 1 |
| S10 | - | - | - | - | 1 N | - | - | - | 1 |
| S11 | - | 1 N | - | - | YCF-115 | - | YCF-115 | YCF-115 | 4 |
| S12 | - | - | - | - | 1 N | - | - | 1 N | 2 |
| S13 | - | - | - | - | - | 1 N | - | - | 1 |
| S14 | 2 N | 1 N | - | YCF-91, 1 N | - | - | YCF-91, 1 N | - | 7 |
| S15 | - | 2 N | - | YCF-80 | - | - | - | - | 3 |
| S16 | - | - | - | - | - | 1 N | - | - | 1 |
| S17 | - | - | - | - | - | YCF-38 | YCF-139 | YCF-38, YCF-66 | 4 |
| S18 | - | - | - | YCF-6 | YCF-11 | - | - | - | 2 |
| S19 | - | - | - | 1 N | 1 N | - | - | - | 2 |
| S20 | 2 N | 1 N | 1 N | YCF-101 | - | YCF-101 | - | - | 6 |
| S21 | 1 N | 1 N | 1 N | YCF-61 | - | YCF-53 | - | - | 5 |
| S22 | - | - | - | 1 N | 1 N | - | - | - | 2 |
| S23 | - | 4 N | 1 N | 2 N | - | - | - | - | 7 |
| S24 | 1N | 1 N | - | 1 N | YCF-50 | - | - | - | 4 |
| S25 | 1 N | - | - | - | YCF-136 | YCF-91 | - | - | 3 |
| S26 | - | - | YCF-10 | YCF-10, YCF-11 | - | YCF-10 | 1 N | YCF-10 | 6 |
| S27 | - | 1 N | - | - | 1 N | 2 N | YCF-10 | - | 5 |
| S28 | 2 N | 4 N | YCF-13 | YCF-12, YCF-13 | YCF-105 | - | - | - | 10 |
| S29 | 1 N | 2 N | YCF-103 | YCF-97 | - | YCF-97 | - | - | 6 |
| S30 | - | 1 N | YCF-138 | YCF-138 | YCF-138 | - | YCF-138 | - | 5 |
| S31 | - | - | - | 1 N | 1 N | YCF-86 | - | YCF-68 | 4 |
| S32 | 1 N | - | YCF-1 | YCF-92 | YCF-1 | YCF-55 | YCF-142 | YCF-1 | 7 |
| S33 | 3 N | 1 N | 1 N | 2 N | 1 N | 1 N | - | - | 9 |
| S34 | 1 N | 1 N | 1 N | YCF-54 | YCF-101 | YCF-100, YCF-76, 1 N | YCF-101 | - | 9 |
| S35 | 1 N | 1 N | - | 2 N | 1 N | 1 N | - | - | 6 |
| S36 | - | - | 1 N | YCF-96, YCF-53, 2 N | YCF-51 | 1 N | - | YCF-53 | 8 |
| S37 | - | - | YCF-61 | - | YCF-73 | - | - | - | 2 |
| S38 | 1 N | 1 N | 2 N | - | - | 1 N | 1 N | - | 6 |
| S39 | - | - | - | - | - | - | YCF-13, YCF-140 | YCF-140 | 3 |

**(Continued Table S1)**

| Nest site | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | Frequency |
|---|---|---|---|---|---|---|---|---|---|
| S40 | - | - | - | YCF-137 | - | - | YCF-137 | - | 2 |
| S41 | - | - | YCF-14 | - | - | - | YCF-14 | - | 2 |
| S42 | 1N | 1 N | - | - | - | - | - | 1 N | 3 |
| S43 | 1 N | - | - | - | - | - | - | - | 1 |
| S44 | - | - | 1 N | - | - | - | - | - | 1 |
| S45 | 1 N | 1 N | - | - | - | - | - | - | 2 |

Note: N: non-marked individual; Frequency: Selected frequency from 2009 to 2016.